

Long- and Short-Term Climate Influences on Southwestern Shrublands

Julio L. Betancourt

Abstract—New findings raise questions about long and short-term climatic effects on Southwestern shrublands. Millennial-scale climate variability during the last glacial may have quickened the pace of evolution for genetically variable shrub species. During the last deglaciation, greater plant water use efficiency due to 30 percent CO₂ enrichment was not enough to offset Holocene aridity, and desert scrub replaced woodlands over much of the Southwestern United States. Likewise, the degree to which present CO₂ enrichment is driving C₃ shrubs into C₄ grasslands is probably a function of interdecadal climate variability. Shrub encroachment accelerated during the 1950's drought, when both winters and summers went dry, and continues under the wet winter-summer dry regime since 1976. Climate is also modulating the spread of exotic annual grasses and introduction of a vigorous fire regime in native shrublands, where none existed before. A combination of biogeographic, historical, experimental, modeling, and monitoring approaches is proposed to predict the ecological outcomes of climate change and direct human impacts.

Interest in global change has produced new insights about the functioning of the Earth's climate system and its interaction with the biosphere. We have rescaled our view of the world to recognize that variability occurs along a continuum of spatiotemporal scales. We have developed and refined tools to measure and understand climate variability, from satellite observations to general circulation models. Our understanding of past climates has increased exponentially, in large part due to advances in geochemistry and generous support for highly collaborative ice core and ocean drilling programs.

In areas occupied by shrublands, aridity has hindered limnological/palynological approaches, yet has provided other unique opportunities to decipher the past. In the arid interior of North America, we have used noble gas concentrations in radiocarbon-dated groundwaters to reconstruct glacial temperatures (Stute and others 1995), fecal pellet diameter in fossil middens to study the evolutionary response of packrat body size to global warming during deglaciation (Smith and others 1995), and carbon isotopes from soil carbonates to discriminate changes in the dominance of C₃ versus C₄ plants (Cerling and others 1991; Cole and Monger 1994; Quade and others 1989). Our knowledge about the past distribution of key shrubs in the Southwestern United States comes almost wholly from packrat middens. The sequence of species departures and arrivals on the

Holocene landscape indicate individualistic responses to changing climate (Betancourt and others 1990). At northern and upper limits, the arrivals are recent enough to confound the distinction between ongoing migration since the end of the Pleistocene and "invasion" driven by fire suppression and overgrazing.

In setting the stage for this symposium on "Shrubland Ecosystem Dynamics in a Changing Environment," I will focus my presentation on a selection of new findings that raise questions about both long and short-term climatic influences on southwestern shrublands. These include (1) the ecological consequences of unusually low atmospheric CO₂ levels (180 to 200 ppmv) during the last glacial, and implications for future CO₂ enrichment effects; (2) discovery that glacial conditions were more variable than previously thought, and how that might alter our thinking about the evolutionary history of key shrubs; (3) increasing recognition that modern climate varies on an interdecadal scale, and the conundrum of discriminating climatic from anthropogenic effects in recent vegetation trends, from shrub encroachment of grasslands to exotic grass invasion of native shrublands.

This brief synthesis updates other recent summaries of climatic effects on arid lands vegetation in the Western United States, including Betancourt and others (1993) and Tausch and others (1993). My intent here is to introduce this audience to the more recent literature, and perhaps inspire new thought about the role of climate in the evolutionary history, ecology and management of North American shrublands.

CO₂ Enrichment Effects: Lessons From the Fossil Record

Knowledge that atmospheric CO₂ increased 30 percent during the last deglaciation (from about 190 to 270 ppmv) (Raynaud and others 1993) and again since industrialization (from 270 to 360 ppmv) has stimulated research linking this greenhouse gas with past, present, and future climate change. The ice core record of atmospheric CO₂ has inspired laboratory experiments that simulate plant responses at subambient (about 180 to 200 ppmv) levels (Polley and others 1993; Polley and others 1994), as well as new paleoecological approaches (Marino and others 1992; Toolin and Eastoe 1993) and interpretations of the fossil record that consider direct CO₂ effects (Cole and Monger 1994; Van de Water and others 1993). Some of these interpretations bear directly on recent claims that modern CO₂ enrichment is at least partly driving encroachment of C₃ shrubs into C₄ grasslands (Idso 1992; Johnson and others 1993; Polley and others 1992; Polley and others, this volume; Tischler and others, this volume; for opposing view see Archer and others

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Julio L. Betancourt is Physical Scientist, U.S. Geological Survey, 1675 W. Anklam Rd., Tucson, AZ 85745.

1995). During deglaciation, mean annual temperatures increased by 5 to 6 °C (Stute and others 1995) and winter precipitation decreased, possibly by more than half of glacial values (Phillips and others 1992). Apparently, the putative increase in water use efficiency due to the 30 percent CO₂ enrichment (Van de Water and others 1994) was not enough to offset increasing aridity, and glacial woodlands were replaced by Holocene desertscrub (Betancourt and others 1990). In water-limited ecosystems such as Southwestern shrublands, questions remain about the relative roles of climate variability, CO₂ fertilization, and overgrazing/fire suppression in shrub invasions and desertification.

Millennial-Scale Variability During the Last Deglaciation

For an evolutionary biologist, it is critical to know the degree, frequency, and rapidity of environmental change during evolutionary time scales. Redistribution of land masses and mountain uplift drives large-scale changes in global climate on scales of 10⁶ years, while changes in the Earth's orbital parameters (Milankovitch) pace changes on scales of 10⁴ and 10⁵ years, including glacial-interglacial cycles. The most recent challenge to paleoclimatologists and paleoecologists stems from increasing recognition of global changes at higher frequencies (10³ years) during the last glaciation.

At the scale of 10³ years, the Greenland ice core record documents more than 20 abrupt, millennial-scale warming events during the last glaciation, referred to as "Dansgaard-Oeschger interstadials" (Dansgaard and others 1993). Warming apparently occurred within decades, followed by gradual return to glacial conditions over hundreds of years. These 2,000 to 3,000-year oscillations occur in series (referred to as Bond cycles), in which the amplitude increases until an unusually cold phase is succeeded by unusual warmth. The extreme cold swings are recorded as major ice-rafting events (coarse debris) in North Atlantic deep-sea sediments, so-called Heinrich events occurring 11,600, 14,500, 21,000, and 27,000 years ago, and two poorly dated events between 36,000 and 70,000 years (Bond and Lotti 1995). In addition, minor ice-rafting cycles synchronous with the cold phase of the Dansgaard-Oeschger temperature shifts have now been identified in glacial sediment from the North Atlantic.

Dansgaard-Oeschger events, Bond cycles, and Heinrich events are not well understood, but may result from transient changes in boundary conditions including surging of continental ice sheets, reversals in ocean thermohaline circulation, short-term increases in atmospheric CO₂, and solar variability (for popular accounts, see Broecker 1995; Kerr 1993, 1996; Lehman 1993). Originally thought to be restricted to Greenland and the North Atlantic, evidence for Dansgaard-Oeschger and Heinrich events now is proposed for key areas in North America, including offshore sediments along the Pacific margin (Behl and Kennett 1996; Kennett and Ingram 1995; Thunnell and Mortyn 1995), mountain glaciation (Clark and Bartlein 1995) and lake levels in the Western United States (Allen and Anderson 1993), and pollen variations in lake sediments from Florida (Grimm and others 1993), a region teleconnected to the

tropical Pacific (and the Southwestern United States) via the subtropical jet stream.

Despite ample evidence for rapid global-scale changes during the last glaciation, involving the climatically important Pacific, the glacial vegetation record for the American Southwest appears relatively monotonous (Betancourt and others 1990; Thompson and others 1993; Van Devender and others 1987). Part of this has to do with the nature of the fossil record: temporally discontinuous packrat midden sequences not necessarily straddling Pleistocene ecotones, where the changes must have been registered, and lake muds with sedimentation rates too slow to log rapid changes in climate and vegetation.

In the near future, one of the greater challenges for Southwestern paleoecologists (and evolutionary biologists) will be consideration of the regional ecological and evolutionary consequences of Dansgaard-Oeschger/Heinrich events. For example, is the unexpected distribution of ploidy/flavonoid races and morphological forms of shadscale (*Atriplex confertifolia*) and four-wing saltbush (*A. canescens*) due to repeated introgression during the shorter and more recent Dansgaard-Oeschger cycles of the last glaciation, as lagging populations hybridized with immigrant genotypes, or is it a product of longer-term glacial-interglacial cycles (Sanderson and others 1990)? To what extent is the explosion of *Atriplex* (Stutz 1978) and other genetically rich genera a function of glacial/interglacial cycles, millennial-scale variability during the last glaciation and/or Holocene aridity? How did climate variability on these different time scales affect (drive) the immigration of creosote bush (*Larrea divaricata*) to North America and subsequent evolution and redistribution of three chromosomal races across the hot deserts of the Southwestern United States (contrast Wells and Hunziker 1976 with Van Devender 1990).

Notwithstanding spectacular advances in climatology past and present, many key questions about past global change remain unresolved. For example, climatologists are polarized over whether or not tropical sea surface temperatures (SST's) are somehow "thermostated" to below 28 °C, or can increase enough to fuel higher atmospheric water vapor concentrations and "global warming" (ICC 1995). The most recent thinking is that the thermostat is maintained by the dynamic ocean-atmosphere coupling that gives rise to east-west SST gradients and the Walker atmospheric circulation in the tropical Pacific (Sun and Liu 1996). Not surprisingly, GCM's used by different groups to simulate global warming from increases in atmospheric CO₂ vary by a factor of two in estimates of tropical warming (Rind 1990).

Conventional wisdom that SST's were the same during the last glacial maximum as the modern ocean (Crowley and North 1991; Rind and Peteet 1985) is now challenged. Strontium/calcium and oxygen isotopes of drowned coral reefs offshore Barbados show that tropical SST's were 5 °C cooler during the last glacial maximum (Guilderson and others 1994). Coral records also show that tropical SST's have varied by 1 to 3 °C during the last few hundred years (Dunbar and others 1994).

Abrupt increases in tropical Pacific SST's have been related to increasing global temperatures since 1976. Linkage to "greenhouse warming" and an accelerated tropical hydrological cycle have been proposed (Graham 1994). Regardless

of their origin, the post-1976 changes bear directly on attempts to detect and explain recent vegetation trends in the Western United States, where regional climate is strongly teleconnected to SST variations in the tropical Pacific on both interannual and interdecadal scales.

Interdecadal Variability and 20th Century Vegetation Change

Evidence for climate behavior on interdecadal scales (15 to 30 years) has been demonstrated empirically from historical climate data sets (Ghil and Vautard 1994; Halpert and Ropelewski 1992; Latif and Barnett 1994; Mann and Park 1994; Mann and others 1995; Miller and others 1994; Rasmussen and others 1990; Trenberth 1990; Xu 1993) and high-resolution (annual) proxies including tree rings, corals, marine and lake sediment varves, and ice cores (Cole and others 1993; Diaz and Pulwarty 1994; Dunbar and others 1994; Ebbesmeyer and others 1991; Jones and others 1996; Linsley and others 1994; Meko and others 1993; Slowey and Crowley 1994; Stahle and others 1993; Stocker and Mysak 1992). These high-resolution proxies provide a context for evaluating the uniqueness of twentieth century climate and thus, for identifying possible anthropogenic influences on recent climate (Diaz and Bradley 1994). Particularly relevant are long-term changes evident in the Southern Oscillation, the flip flop in sea surface pressure patterns across the equatorial Pacific that marks alternation between El Niño (warm Pacific) and La Niña (cold Pacific) States.

The importance of interdecadal variability is underscored by the unusual frequency of El Niños during the last 20 years (since 1976), when the Southern Oscillation locked into the negative, warm (El Niño) phase, and the length of the most recent El Niño (1991 to 1995), which topped the prolonged 1911 to 1915 and the 1939 to 1942 events. Based on time series modeling, Trenberth and Hoar (1996) suggest that the unusual string of El Niños since 1976 and the protracted 1991 to 1995 event should occur only once every thousand years. This begs the question of whether greenhouse warming or natural climate variability shoulders the blame.

Global average tropospheric temperatures have been rising during the past century, with the most recent portion of record showing a sharp rise since the mid-1970's. Empirical evidence suggests that this sharp rise, roughly half of the 0.6 °C long-term global warming attributed to the Greenhouse Effect, may be due to an enhancement of the tropical hydrologic cycle driven by increasing tropical SST's. Graham (1994) has reproduced the global temperature record since 1976 with an atmospheric model forced with observed SST's (see also Kumars and others 1994). He suggests that the tropical Pacific is now operating at a higher mean temperature, not simply experiencing more frequent El Niño events.

In the Southwest, El Niño conditions are associated with stormier winters and springs (Andrade and Sellers 1988) and drier summers (Harrington and others 1992), the opposite considered true for La Niña years. Using tree rings from Oklahoma, Texas and northern Mexico, Stahle and others (1993) have shown that the influence of the Southern Oscillation on North American winters also may be subject to changes in the frequency and amplitude of both warm and cold events on decadal to multidecadal timescales. Forest

fire-Southern Oscillation relations in the Southwest inferred from fire scars show a similar interdecadal behavior (Swetnam and Betancourt 1990, 1992). Twentieth century climatic trends stemming from the interdecadal behavior of the tropical Pacific include wet winters in the early part of the century, a mid-century dry period, and wet winters and erratic summers since 1976. The 1950's drought is the most extreme event of recurrent widespread drought in the southern United States during the past 300 years (Betancourt and others 1993; Meko and others 1993; Stahle and Cleaveland 1988).

At issue is the degree to which recent vegetation changes, such as shrub invasions, can be attributed to climatic variability, compared to overgrazing and fire suppression (Bahre and Shelton 1993; Grover and Musik 1990; Neilson 1986). The debate is confounded by the fact that progressive range deterioration since 1870 has been inferred from historical data (Bahre and Shelton 1993), while long-term monitoring indicates substantial range improvement with wetter conditions following the 1950's drought (McCormick and Galt 1994). Such ambiguity will continue to plague ecosystem research and management, especially if the trend towards a warmer Pacific resumes after the 1996 La Niña (cold Pacific) event, which is producing extreme drought across northern Mexico, the southern High Plains, and the Southwestern United States.

For example, climate appears to be regulating the invasion of red brome (*Bromus rubens*) in the upper Sonoran Desert of central and southern Arizona, an alarming phenomenon. Wetter winters since 1976 have encouraged the spread of this winter annual, and the buildup of fine fuels in native shrublands. Consequently, large fires have become chronic in desert communities that burned rarely only 20 years ago (Harper and others, this volume; McLaughlin and Bowers 1982). Many desert plants, such as saguaros (*Carnegiea gigantea*), grow slowly and recruit episodically; on decadal timescales, desert fires have irreversible consequences. A shift to drier winters and wetter summers might slow the red brome invasion, while encouraging exotic summer annuals like African buffel grass (*Cenchrus ciliare*), which becomes flammable in the fall. It is unclear what remedy can be applied, if any. One could propose an aggressive program of fire suppression in the Sonoran Desert. This might be viewed as inconsistent by a ranching community that is increasingly accepting fire as an ecological process capable of holding shrub invasion of grasslands at bay.

Conclusions

In assessing ecosystem dynamics in a changing environment, there is always the temptation to develop massive simulation models that couple many physical and biological processes. Such models require a detailed understanding of all the feedbacks and constraints that limit the range of the output, including external forcing such as climate variability. Alternatively, we can study interactions between selected properties of ecosystems during extreme events or conditions, and look for predictable behavior (Mann 1995). Such phenomological studies include investigation of processes along climatic (and land use) gradients; century to millennial scale reconstructions of plant migration and

ecotonal shifts; reconstruction of demographic trends (Parker 1993) and changes in community composition using repeat photography and remote sensing (Eve and Peters, this volume; Lancaster and others, this volume; Sanders and Sharp 1995; Walker and others, this volume); monitoring efforts persistent enough to capture extreme events (Goldberg and Turner 1984; Havstad and Schlesinger, this volume; Huenneke, this volume); simulation of extreme conditions in experimental research (de Soyza and others, this volume; Heydari and others, this volume; Polley and others, this volume; Tischler and others, this volume; Virginia and Reynolds 1995; Weltzin and McPherson 1995); and modeling approaches that simulate the appropriate spatiotemporal scales of disturbance (Ludwig and others, this volume; Reynolds and Virginia 1995; Wiegand and others 1995; Wiegand and Milton, this volume). In addition, one could also promote biogeographic approaches that compare areas with opposing interdecadal climatic trends, such as the Southwestern United States and the Pacific Northwest, or areas where the same species (or similar genera) have experienced different climatic and land use histories. For example, why do mesquite (*Prosopis* spp.) and creosote bush (*Larrea* spp.) tend to be so widespread, dominant, and invasive wherever they occur in both North and South America? Clearly, some of our questions about ecosystem dynamics in a changing environment may find answers in comparative studies that employ similar approaches in shrublands worldwide.

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